A NEW SPECIES OF MACHAERIDIAN FROM THE SILURIAN OF PODOLIA, USSR, WITH A REVIEW OF THE TURRILEPADIDAE

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ABSTRACT. Machaeridians are enigmatic marine fossils, known from rocks of Ordovician to Carboniferous age. *Turrilepas modzalevskae* sp. nov., from Podolia, Ukraine, USSR, is only the second turrilepadid machaeridian species to be represented by an articulated assemblage. It provides unequivocal evidence for the presence of minute marginal spines, and demonstrates the relationship between these spines and the ornament of the outer sclerite surface. A standardized system of terminology for turrilepadid machaeridians is presented, based on examination of many specimens of *Turrilepas wrightiana* (de Koninck) from the Wenlock of Britain, together with undescribed Canadian silicified material. The anterior structure of turrilepadids and plumulitids is very similar, both lacking outer series sclerites on the first two segments. The Family Turrilepadidae comprises the genera *Turrilepas* Woodward, *Deltacoleus* Withers, *Clarkeolepis* Elias, *Spinacoleus* Schallreuter, and *Mojzcalepas* Dzik. All but *Turrilepas* are inadequately known.

DURING a visit to the Natural History Museum in 1988, J.M.A. discovered a specimen in the palaeontological collections labelled *Lepidocoleus* sp., collected from Podolia in 1983 by L.R.M.C. It was recognized that the specimen belonged in fact to *Turrilepas* Woodward, 1865, and was important because it represented only the second unequivocal record of the genus. The type species is from the British Wenlock.

Turrilepas modzalevskae, described herein, is only the second turrilepadid species to be represented by an articulated specimen. Examination of the many specimens of *Turrilepas wrightiana* in the Natural History Museum, together with knowledge derived from study of undescribed North American silicified faunas by J.M.A. has resulted in a more thorough understanding of the arrangement and structure of the turrilepadid scleritome, a subject to which little new information has been added since T. H. Withers's seminal work of 1926. An attempt is made to standardize descriptive terminology, and the status of the currently recognized turrilepadid taxa is reviewed. A historical review of machaeridian study and a discussion of recent systematic problems is presented elsewhere (Adrain in press). Illustrations of silicified sclerites are scanning electron micrographs. Illustrated calcareous specimens were blackened and given a light coating of ammonium chloride sublimate prior to photography. Illustrated specimens are housed in the Natural History Museum, prefixed BM(NH), and the palaeontological collections of the University of Alberta, prefixed UA.

LOCALITY AND STRATIGRAPHY

Podolia lies in the centre of eastern Europe; until the Second World War it was in Poland and since then it has formed part of the Ukraine. Access has been difficult, but in May 1983 the Silurian Subcommission was invited to visit and collect from the sequence, which consists of nearly flat-lying beds of mostly late Silurian and early Devonian age all unconformably overlain by the Cretaceous (Koren *et al.* 1989). The locality of the new species of *Turrilepas*, *T. modzalevskae*, lies in a natural outcrop on the left slope near the mouth of the Smotrich River, near Tsvicklevtsy village (Tsegelnjuk *et al.* 1983, Stop 4, p. 75). Here the Ustje Member of the Bagovitsa Formation is exposed to 9·5 m and overlain conformably by Konovka Formation, which is composed of a lower

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Goloskov Member (11·5 m) and an upper Shutnovsky Member (17·9 m), in turn overlain by the Sokol Member of the Tsvicklevtsy Formation which is seen to 19 m. The new *Turrilepas* undoubtedly came from the Konovka Formation, but since the single specimen was found loose, it is uncertain whether it came from the Goloskov or the Shutnovsky Member. Both members yield a very similar shelly fauna dominated by the brachiopods *Atrypella*, *Microsphaeridiorhynchyus*, *Protochonetes*, and *Sphaerirhynchia*, and in other accounts (e.g. Koren *et al.* 1989) the members are not used. The age of the Konovka Formation is also securely fixed as basal Ludlow (lower Gorstian Stage), based not only on the brachiopods, but also on the ostracods present (Koren *et al.* 1989, fig. 108); however, there are no useful records of graptolites from that part of the Podolian succession.

TERMINOLOGY

There is no standard system of terminology for description of machaeridian sclerites and sclerite assemblages, although Jell (1979) and Schallreuter (1985) have made progress. Withers (1926) provided a comprehensive set of terms. His opinion was, however, that machaeridians were sessile, attached to the substrate by one end of their assemblage, and capable of opening and closing their assemblage along what he termed the 'free margin'. This interpretation of function and orientation now seems highly improbable (Jell 1979; Schallreuter 1985; Dzik 1986), and hence Withers's descriptive terms are largely obsolete. It is now generally accepted that machaeridians were vagile, that the more modified end of their assemblages was anterior, with the sclerites imbricating posteriorly, and that the median line along which opposing series sclerites meet in all known machaeridians was dorsal.

This orientation is followed here, but problems arise when comparing isolated sclerites, as homologous parts may be held in completely different orientations in the assemblages of different machaeridians. Furthermore, there is often sufficient serial variation along the scleritome that anteriorly placed, midbody, and posteriorly placed sclerites will have different orientations with respect to the general orientation of the whole assemblage. It has therefore been found necessary to adopt conventions when referring to particular aspects of sclerites. These conventions follow from the most general orientation of the sclerite and facilitate comparisons between differently arranged taxa, but do not necessarily correspond to what would have been the actual orientation of the part in a particular living machaeridian.

Terms referring to the entire scleritome

The term *scleritome* (Bengtson 1985) is used to refer to the organizational plan of the entire assemblage for a given species. It is recommended that *sclerite assemblage* (Jell 1979) be used to refer to an actual set of associated sclerites recovered from the fossil record. They are together given preference over 'strobilus' (Pope 1975). The division of the scleritome into the longitudinal sectors 'head,' 'thorax,' and 'abdomen' (Dzik 1986) should be discontinued, as it carries organizational and phylogenetic connotations which are thus far unsupported. Likewise, the neutral term *sclerite* is preferred over 'elytrum' (Jell 1979; Dzik 1986).

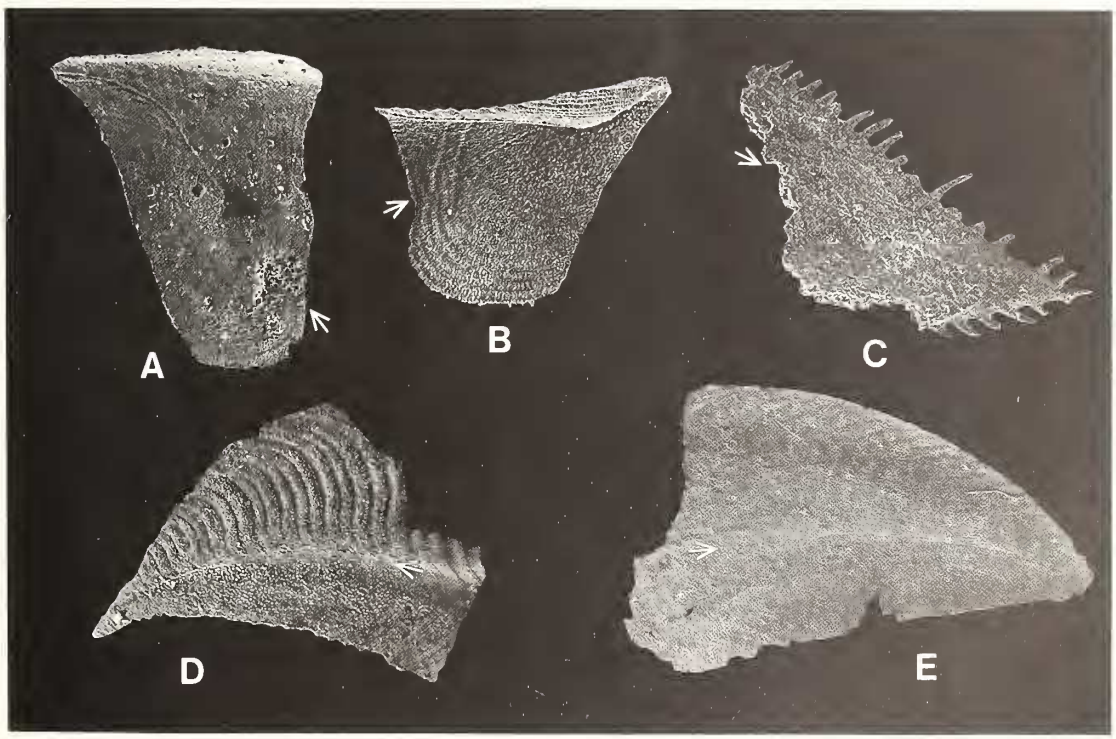
The longitudinal columns of a particular scleritome are referred to as *sclerite series*. Biserial machaeridians have left and right series. Quadriserial machaeridians have left and right *inner* and *outer* series. The rows of the scleritome may well correspond to particular body segments, if its fully segmented nature is indicative of true, and not merely functional, metamerism. It is not possible to evaluate this suggestion further, however, given our present state of knowledge of the group. Hence, the term 'segment' is used here in a phylogenetically neutral sense. When distinguishing between sclerites within a given series or set of series, reference should be made, where possible, to the sclerites of the *xth segment*, measured from the anterior of the scleritome.

Terms referring to individual sclerites

Bengtson (1978) has determined that machaeridian sclerites are composed of two distinct layers. An *outer layer* is composed of dense calcite, in which growth lines may often be visible (see Pl. 2, fig. 10),

and from which the rugae are formed (terms defined below). The *inner layer* is composed of distinct, densely packed lamellar elements which correspond closely to the granular texture of the inner sclerite surface. The layers may vary in thickness, depending upon the taxon in question. Bengtson (1978) noted that in the turrilepadid he investigated, two distinct layers did not appear to occur. In many silicified turrilepadid sclerites, the outer surface between the rugae has exactly the same granular texture as the inner surface. This indicates that the inner sclerite layer made up almost the entire sclerite thickness, with the outer layer confined to the rugae and not deposited between them.

Some of the following terms are illustrated in Text-figures 1–3. The *outer surface* of a sclerite is defined as that which bears the *rugae*. Rugae are prominent, ridge-like features, evenly spaced and developed parallel to the fine *growth lines*, apparently through deposition of additional material of the outer sclerite layer at specific growth increments. Rugae terminate before they reach the sclerite margin. Figured examples in which this appears not to be the case (e.g. Schallreuter 1985, pl. 2, figs 1–3) represent artefacts of poor preservation. Similar preservation has been observed by the authors in silicified material from the Canadian Arctic. Relatively coarse silicification often results in poorly preserved margins. The rugae seem to be more amenable to silicification in these conditions than the material of the margin and hence they are sometimes preserved while the margin lateral to them is not. They then protrude from the margin of the fossil sclerite, creating a false impression of having been extended into marginal spines in the living animal.



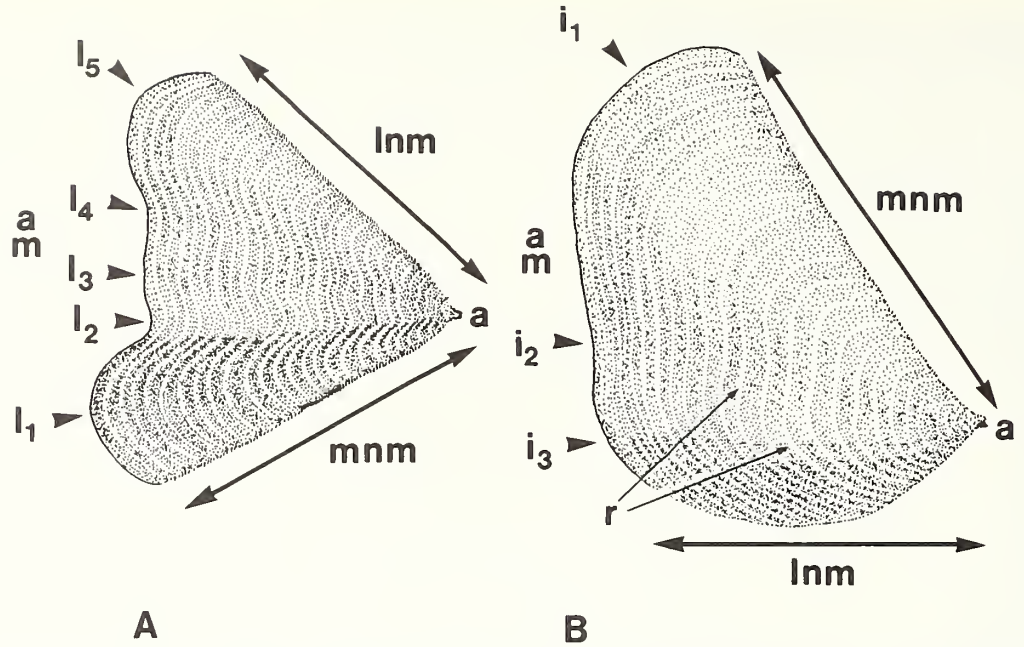
TEXT-FIG. 1. Silicified machaeridian sclerites from the Mackenzie Mountains, Northwest Territories, Canada, to illustrate the *inner groove* possessed by all machaeridian sclerites. The groove runs from the apex, and its anterior extent is indicated by an arrow in each case. All are scanning electron micrographs of the inner surface. A, UA 8125, left sclerite belonging to a new family of the Order Lepidocoleomorpha, AV 4 126, ×37. B, UA 8126, right tongued lepidocoleid, AV 5 58–60, ×36. C, UA 8127, outer right turrilepadid, AV 5 58–60, ×37. D, UA 8128, outer right plumulitid, AV 4 126, ×18. E, UA 8129, outer left plumulitid, AV 5 58–60, ×10. See Over and Chatterton (1987) for locality information.

The *inner surface* has a finely granular texture, reflecting the regular arrangement of calcite elements in the inner sclerite layer. A single *muscle scar* is borne on the inner surface, although in some sclerites, particularly small ones and most Plumulitidae, it may be difficult to discern. A narrow groove runs anteriorly from the apex on the inner surface of all machaeridian sclerites (see Text-fig. 1). The function of this groove is not yet clear, but its universal occurrence suggests an intimate relationship with some fundamental aspect of machaeridian soft part anatomy. It is termed, for the time being, the *inner groove*. The *umbo* is the site of initial sclerite growth. It is usually located at the *apex*, but may sometimes be set somewhat forward, creating initially concentric growth lines (see Text-fig. 2D). The apex of turrilepadid sclerites is very often ornamented with a bifid *apical spine*, although this structure is frequently broken off before or after preservation. Some lepidocoleids also have an apical spine, but it seems never to have accessory spines developed upon it (see below), and invariably has a simple, not bifid, tip. All machaeridian sclerites have three margins (see Text-fig. 3). The *accreting margin* runs parallel to the growth lines and rugae, and is the front of deposition of new sclerite material. It may be further subdivided by folding of the sclerite in various types of machaeridians. The two *non-accreting margins* run from the apex to the edges of the accreting margin. The *medial margin* is that which lies closest to the dorsal midline of the assemblage, and its complement on the opposite side of the sclerite is the *lateral margin*. Many sclerites are folded about an angle which runs anteriorly from the apex to the accreting margin. This is the *longitudinal angle* (see Text-fig. 2C). When it occurs, it divides the accreting margin into *medial* and *lateral* parts. All known turrilepadids have *marginal spines* on the non-accreting margins. These spines are often continued on the lateral aspects of the apical spine, and are quite independent of the spacing of either the growth lines or the rugae, contrary to the claim of Dzik (1986, p. 119). In fact, the growth lines bend anteriorly near the sclerite margin, and in *Turrilepas modzalevskae*, can actually be seen to transect the marginal spines (see Pl. 2, fig. 10). This indicates that the marginal spines are formed from a different material to that which forms the outer surface. They seem either to have been formed from an accessory material deposited along the non-accreting margins as growth proceeded, or more likely from the material of the inner sclerite layer. Turrilepadid sclerites often have a distinct *doublure* (see Text-fig. 2B, E, H) preserved around the margins on the inner surface. The depositional and crystallographic characteristics of this feature are obscure, as it has thus far been observed only in well preserved silicified specimens. It is not clear whether or not it is a universal feature of turrilepadids. When it occurs, however, it is almost identical in texture to the marginal spines, and when viewing the inner surface, these spines seem to be lateral extensions of the doublural material. It seems likely, therefore, that the doublure is always present but often, like the marginal spines, not well expressed.

The pattern of rugae on the outer sclerite surfaces is constant within a sclerite type of a single species, and is therefore of much potential taxonomic value. To facilitate description and comparison, a system of numbering the inflections in the course of the rugae has been devised (see Text-fig. 3). This system is based upon sclerites of the genus *Turrilepas*, the best known turrilepadid. The general pattern and number of inflections seems on present evidence to be universal throughout Turrilepadidae, but this will require corroboration through further study. Numbering begins from the medial margin. Five inflections are present on inner sclerites, labelled I_1–I_5. The upper case 'I' is used for inner sclerites, and an 'R' or 'L' may be appended to distinguish between right or left sclerites. Outer sclerites feature only three inflections, labelled in lower case to distinguish them from inner sclerites, i_1–i_3. Thus, for example, I_1L refers to the first inflection of an inner left sclerite, while i_2R refers to the second inflection of an outer right sclerite. Note that although I_2 often coincides with the longitudinal angle of the inner sclerites (see, for example, Text-fig. 3A), this is not always the case, and the two terms refer to separate and distinct features.

Some combinations of features that may serve to characterize and distinguish between taxa include the degree to which each of the inflections is expressed, and the relationship between the longitudinal angle and the inflections. This system of numbering is adequate for reference to the Family Turrilepadidae. Some modification will be required for the plumulitids and lepidocoleomorphs, and will be presented elsewhere.

TEXT-FIG. 2. Silicified machaeridian sclerites from the Wenlock of the Mackenzie Mountains, Northwest Territories, Canada. All sclerites are from horizon AV 5 58–60, except I, which is from AV 2 248·8 (see Over and Chatterton 1987 for details). All are scanning electron micrographs. A–C and E–I are turrilepadids, D is a plumulitid. A, UA 8130, outer left sclerite, outer view, ×37. B, UA 8131, inner right sclerite, inner view, ×36. C, UA 8132, inner left sclerite, outer view, ×40. D, UA 8133, inner right plumulitid sclerite, inner view (ridges are not rugae, but rather the impressions of the rugae borne on the outer surface), ×40. E, F, UA 8134, outer right sclerite, inner and outer views, ×19. G, H, UA 8135, outer left sclerite, outer and inner views, ×37. I, UA 8136, inner right sclerite, outer view, ×20. *a*, apex, *am*, accreting margin, *as*, apical spine, *d*, doublure, *la*, longitudinal angle, *ms*, muscle scar, *msp*, marginal spine, *u*, umbo.



TEXT-FIG. 3. Sclerites belonging to *Turrilepas wrightiana* (de Koninck), illustrating some of the terminology introduced. A, inner right sclerite. B, outer left sclerite. *a*, apex; *am*, accreting margin; *lnm*, lateral nonaccreting margin; *mnm*, medial nonaccreting margin; I_x, *xth* inflection of rugae, measured from medial margin, of inner sclerite; i_x, *xth* inflection of rugae, measured from medial margin, of outer sclerite; *r*, rugae.

SYSTEMATIC PALAEONTOLOGY

Class MACHAERIDIA Withers, 1926
Order TURRILEPADOMORPHA Pilsbry, 1916
Family TURRILEPADIDAE Clarke, 1896

Genera included. Turrilepas Woodward, 1865; *Deltacoleus* Withers, 1926; *Clarkeolepsis* Elias, 1958; *Spinacoleus* (= *Rugacoleus*) Schallreuter, 1985; *Mojczalepas* Dzik, 1986.

Diagnosis. Scleritome tightly articulated; sclerites usually large, thick, coarsely rugose; most sclerites with minute to robust bifid apical spine and multiple simple spines on non-accreting margins; mid-scleritome inner sclerites usually with longitudinal angle of about 90 degrees, sometimes more obtuse; medial area of inner left sclerites approximately twice that of inner right sclerites; rugae of inner sclerites usually with five inflections; rugae of outer sclerites with three inflections. For a given segment with four sclerites (i.e. any segment from 3 backwards), the outer sclerites overlap the inner sclerites on each side, and the medial portion of the inner right sclerite overlaps that of the inner left sclerite.

Remarks. It has not previously been appreciated that spinose non-accreting margins and apical spines are features which appear to occur in most turrilepadids. This is certainly because these features sometimes require extremely good preservation to remain evident. They are absent, for instance, from most of the *Turrilepas wrightiana* material from Dudley. Knowledge, however, of Canadian silicified material upon which detail is preserved to an exquisite degree, strongly indicates they are a constant feature. This is corroborated by the fact that in almost all of the Dudley

T. wrightiana specimens, the sclerite margins are either worn or broken off. Withers (1926, p. 41) did note the occurrence of marginal spines on some well-preserved specimens, particularly BM(NH) 59164. Reinvestigation of this specimen (see Pl. 1, figs 5, 7, 8) has shown that the spines are quite obvious. It must be emphasized that, contrary to occasional appearance (see for example BM(NH) 59406, Pl. 1, fig. 10), those Dudley specimens from which marginal spines appear to be absent have margins which have either been poorly preserved, have been broken prior to preservation, or most commonly have been broken and scored away during preparation in the nineteenth century. The apices of almost all of the sclerites collected from Dudley are missing. An exception is a mid-scleritome right inner sclerite on specimen BM(NH) 59406 (Pl. 1, fig. 10), which demonstrates unequivocally the presence of a minute, bifid apical spine.

Dzik (1986, fig. 4) has figured a poorly preserved sclerite from a Polish erratic boulder of Llanvirn age. he has made the following claims for this specimen: (1) that it is an outer plumulitid sclerite; and (2) that the marginal spines of the specimen coincide with the rugae. More material would be necessary to evaluate this taxon with any confidence, but the sclerite almost certainly represents a turrilepadid. Coincidence of the marginal spines and rugae cannot be properly evaluated on the basis of the published evidence, since Dzik did not figure the outer sclerite surface, upon which the rugae are borne. Faint ridges are evident on the inner surface, and these do appear broadly to match the marginal spines. It is possible that in particular sclerites the spacing of rugae may fortuitously approximate that of the marginal spines. The point that bears emphasis is that all other published illustrations of turrilepadid sclerites clearly indicate that there exists no general one-to-one relationship between the features, and their spacing, while it may occasionally match, is independent.

Genus TURRILEPAS Woodward, 1865

Type species. Chiton wrightiana de Koninck, 1857, from the Much Wenlock Limestone Formation of Dudley, West Midlands. By monotypy.

Other species. T. modzalaevskae sp. nov.

Diagnosis. Turrilepadid machaeridians with minute apical spines; very small marginal spines, two or more occurring between each ruga; large, robust sclerites; twenty-five or more rugae on a single mature sclerite; I_1–I_5 all well expressed; I_1 L sharp and angular, I_1 R broadly curving; i_1–i_3 all well expressed, i_2 generally shallow; large, deep muscle scars on inner sclerites; scleritome subrectangular in mid-body cross section, with horizontal dorsal aspect and slightly ventromedially sloping lateral aspects.

Remarks. Only the type species and *T. modzalevskae* are assigned with certainty to this genus. Hall and Clarke (1888) erected eight new Devonian species, four of which were based upon single sclerites. This material requires re-examination before any taxonomic conclusions can be reached. *Turrilepas withersi* Elias and *T. japonicus* Kobayashi and Hamada both seem closer to *Deltacoleus*, discussed below. Both species, however, are at present too poorly known for use in comparative studies. Withers (1926) considered that material from Gotland figured by Aurivillius (1892) belonged to *T. wrightiana*. Bengtson (1979) listed the occurrence of *T.* cf. *wrightiana* and *T.* n. sp. from the Wenlock of Gotland, but the Gotland fauna remains to be investigated.

Turrilepas wrightiana (de Koninck, 1857)

Plate 1, figs 4, 5, 7, 8, 10–12; Plate 2, figs 6–9, 11–14

1857 *Chiton wrightianus* de Koninck, p. 199, pl. 1, fig. 2*a–c*.

1926 *Turrilepas wrightiana* (de Koninck); Withers, p. 37, pl. 5, figs 1–6; pl. 6, figs 1–8 (with full synonymy).

?1978 *Turrilepas* cf. *wrightiana* (de Koninck); Schrank, p. 10, pl. 1, fig. 3; pl. 2, figs 1 and 2; pl. 3, figs 1–3; pl. 4, fig. 1.
?1979 *Turrilepas* cf. *wrightiana* (de Koninck); Bengtson, p. 211.
1986 *Turrilepas wrightiana* (Koninck); Dzik, p. 120, fig. 1B.

Holotype. BM(NH) I16283 (Pl. 1, Fig. 11).

Localities and distribution. Known from the Much Wenlock Limestone Formation, Dudley and Malvern; possibly occurs in the Wenlock of the island of Gotland, Sweden and an upper Wenlock erratic boulder from the island of Rügen, Baltic area, German Democratic Republic.

Diagnosis. A species of *Turrilepas* with at least twenty-six segments; marginal spines on medial non-accreting margins of inner sclerites spaced from two to four between each ruga; minute apical spines; length of accreting margin of outer sclerites subequal to length of longitudinal angle of outer sclerites.

Remarks. Schrank (1978) has figured some sclerites from an erratic boulder from the East German Baltic region, assigned to the upper Wenlock on the basis of the associated trilobite fauna, as *Turrilepas* cf. *wrightiana*. The sclerite illustrated in his plate 1, figure 3 does not belong to *Turrilepas*, but to another unnamed turrilepadid form, sclerites of which are known by the authors to occur in the Wenlock of northern Canada. The remainder certainly belong to *Turrilepas*. In number and spacing of marginal spines, the two inner sclerites figured by Schrank (1978, pl. 2, figs 1 and 2; pl. 3, fig. 1) resemble *T. wrightiana*, although the outer surface of a typical inner sclerite was not figured. The two outer sclerites, however, (Schrank 1978, pl. 3, figs 2 and 3) seem closer to *T. modzalevskae* in general shape. Further specimens would be required to determine the specific identity of this material.

Anterior structure. Withers (1926, p. 40) provided a discussion of the structure of the anterior end of the scleritome of *T. wrightiana*. His examples were specimens BM(NH) 59164 (Pl. 1, figs 5, 7, 8, 12) and BM(NH) 47871 (Pl. 2, figs 12–14), the anterior of which he exposed through careful preparation. At the anterior of both of these specimens there lies a small, almost flat sclerite with an odd orientation. This was interpreted by Withers as one of a pair of 'proximal' sclerites, the anteriormost sclerites that were supposed to function in attachment of the machaeridian to the substrate. We regard neither of these specimens as being true representations of the actual scleritome arrangement. BM(NH) 47871 has very obviously been disturbed, and although many of the modified anterior sclerites are present, the assemblage has been compacted, the

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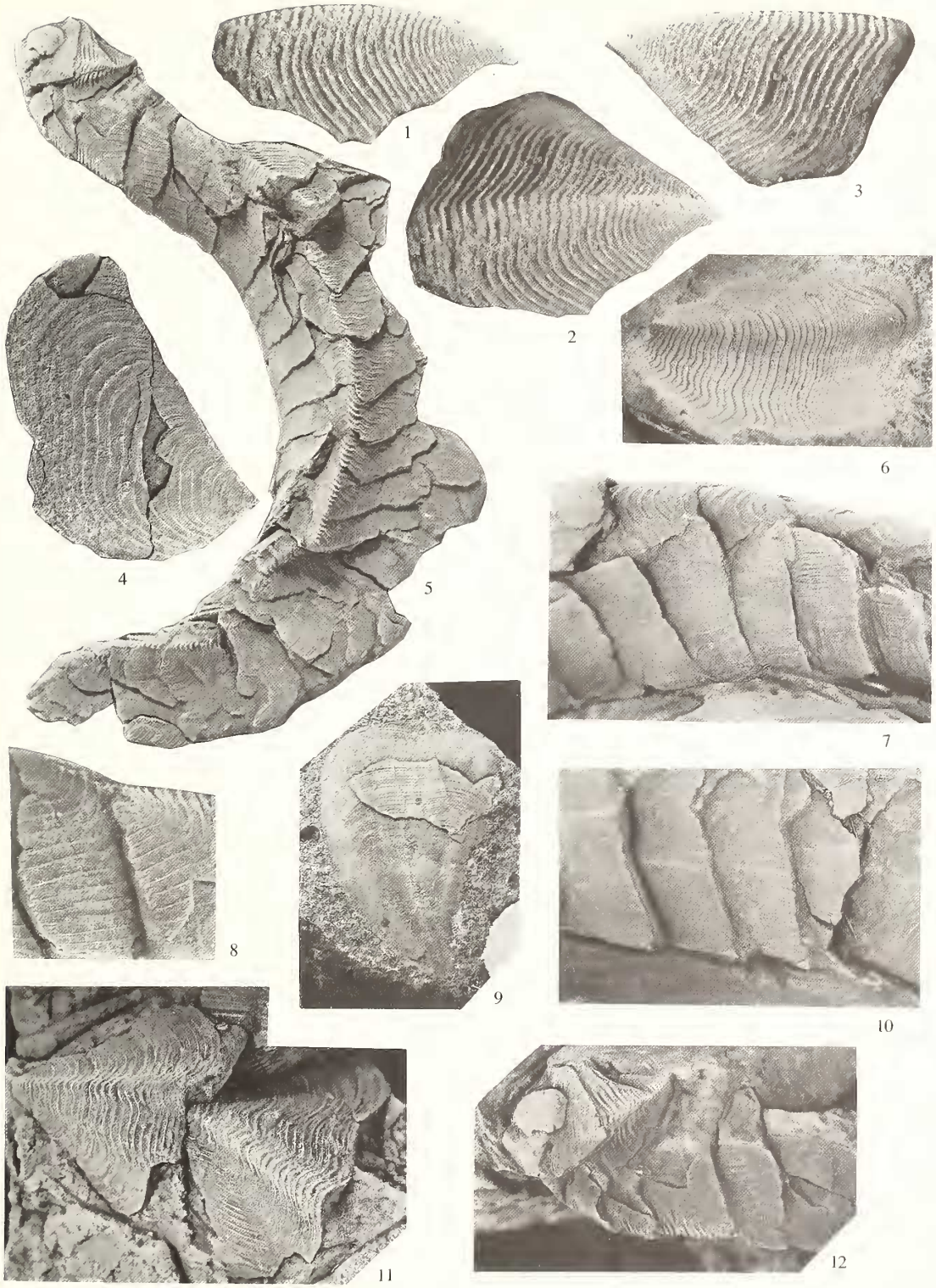
EXPLANATION OF PLATE 1

Figs 1–3. *Deltacoleus crassus* Withers, 1926. Medial, dorsolateral, and lateral views of holotype BM(NH) In23708, inner right sclerite, Balclatchie Group, Balclatchie, Upper Ordovician, ×9.

Figs 4, 5, 7, 8, 10–12. *Turrilepas wrightiana* (de Koninck, 1857). 4, BM(NH) I16308, left outer sclerite, view of outer surface. Wenlock Limestone, Malvern, Middle Silurian, ×5. 5, 7, 8, 12, BM(NH) 59164, nearly complete assemblage, Wenlock Limestone, Dudley, middle Silurian; 5, entire specimen, dorsolateral view, ×2·5; 7, detail from mid-body, dorsal view, note marginal spines, ×5; 8, detail from anterior of assemblage, dorsolateral view, note marginal spines, ×6; 12, detail of anterior end of assemblage, note loss of outer right series and truncation of anterior end of assemblage, ×4. 10, BM(NH) 59406, Wenlock Limestone, Dudley, Middle Silurian, detail from midbody of articulated assemblage, right lateral view, note apical spines, ×4. 11, BM(NH) I16283, holotype, Wenlock Limestone, Dudley, Middle Silurian, right inner and left inner sclerites, Wenlock Limestone, Dudley, Middle Silurian, ×3·5.

Fig. 6. External mould, BM(NH) In23673, assigned to *Deltacoleus crassus* by Withers (1926), but of indeterminate affinities. Inner left sclerite, Balclatchie Group, Dow Hill, Upper Ordovician, ×4.

Fig. 9. BM(NH) In23737, assigned to *Deltacoleus crassus* by Withers (1926), in fact a plumulitid. Outer right sclerite, internal mould with sclerite fragment, view of outer surface, Stinchar Limestone, Aldons, Middle Ordovician, ×4.



ADRAIN *et al.*, *Deltacoleus crassus*, *Turrilepas wrightiana*

relationships between sclerites distorted, and some sclerites lost. BM(NH) 59164 is likewise partially complete, but is missing almost all of its anteriormost sclerites, in addition to the complete right outer series for the anterior half of the sclerite assemblage.

A specimen that provides what appears to be an accurate idea of the anterior structure is known, however. This is BM(NH) I16282 (Pl. 2, figs 6–9, 11), a specimen mentioned but not figured by Withers (1926, p. 38). The outer left series is concealed by the matrix in this example, but all other anterior sclerites seem to be present. The structure of the specimen is described below.

Inner right series sclerites of segments 1–7 are present. Outer right series sclerites of segments 3–6 are present, but some are fractured and fragmentary. Inner left series sclerites 1–5 are present, and an inner left sclerite of an indeterminate more posteriorly placed segment is also evident, displaying a relatively long, bifid apical spine (see especially Pl. 2, fig. 9). Anteriorly in the sclerite series, the inner right sclerites tend to flatten out, and the sclerite of segment 1 all but lacks a longitudinal angle. Conversely, the inner left sclerites become increasingly folded, the longitudinal angle becoming acute. The inner left sclerites of segments 2 and 3 are intact on the specimen. The sclerite of segment 1 has been broken just beneath its longitudinal angle (see Pl. 2, fig. 11), and the lateral portion has folded inward, giving the longitudinal angle a slightly more acute appearance than is in fact the case. The outer right sclerites begin with segment 3, and except for a slight increase in the length of the accreting margin posteriorly in the series, the initial segment is of very similar form to successive ones in the series.

The sclerites of segment 1 are distinctive. The right sclerite has a very wide accreting margin relative to the length of the longitudinal angle. Both sclerites have extremely closely spaced rugae. The inner sclerites of segment 2 are intermediate in morphology between those of segments 1 and 3. By segment three, the sclerites have attained the general form of successive sclerites in their respective series, and the major changes thereafter are restricted to the longitudinal angles moving towards a stable value of approximately 90 degrees.

As regards Withers's example, BM(NH) 47871, the 'proximal plate' with the anteriorly directed apex at the anterior of the assemblage (Pl. 2, fig. 12) is almost certainly the inner left sclerite of one of the anterior segments, possibly 2 or 3, with most of its lateral portion broken off just beneath the longitudinal angle (compare with the fractured segment 1 sclerite in Pl. 2, fig. 11). The sclerites of segment 1 have been lost, and the broken inner left sclerite has been displaced to overlie the accreting margin of the inner right sclerite of segment 2. The inner left sclerite of this segment is intact and in proper spatial relation to its right side counterpart. All of these sclerites, however, have been compacted and slid backward on the truncated assemblage, so that they sit atop an inner right sclerite (see Pl. 2, fig. 13), probably of segment 4.

Comparison of Plate 2, figure 6 with Jell's (1979) figure 4D reveals an essential similarity in structure between the segment 1 sclerites of turrilepadids and those of plumulitids. The sclerites are all but identical in shape and the course of the rugae. Furthermore, both families lack outer series sclerites on the first two segments. Jell's (1979) material established this fact for plumulitids, while the present material provides strong evidence for this condition in turrilepadids.

Accretionary growth. It is notable that within a given sclerite assemblage, all sclerites appear to bear approximately the same number of rugae. On specimen BM(NH) I16282, described above, for instance, the inner left sclerite of segment 1 has twenty-seven discernible rugae. The inner right sclerites of segments 1 and 2, both of which are incomplete, have nineteen and eighteen rugae respectively. The inner left sclerite of segment 4 has twenty-five rugae, as does the inner right sclerite of segment 5. The outer right sclerite of segment 5 is incomplete, but has twenty-four discernible rugae. The rugae are very closely spaced on sclerites of the first

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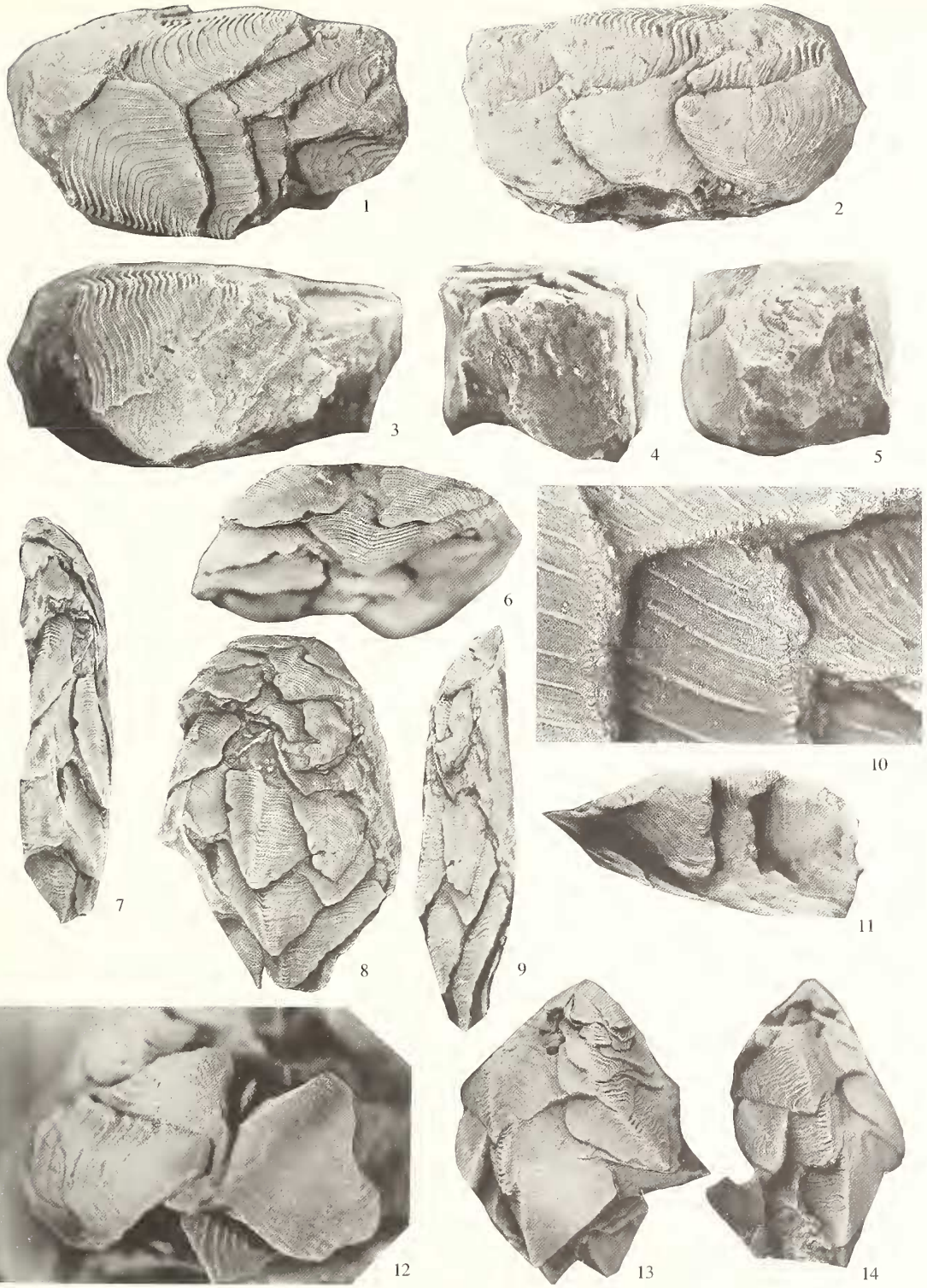
EXPLANATION OF PLATE 2

Figs 1–5, 10. *Turrilepas modzalevskae* sp. nov. BM(NH) In63310, Lower Ludlow, Konovka Formation, Podolia, Ukraine, USSR, holotype. 1, dorsal view. 2, right lateral view. 3, left lateral view. 4, posterior view. 5, anterior view. All ×4. 10, detail of medial aspects of inner sclerites, note rugae, growth lines, marginal spines, and manner in which growth lines transect marginal spines, ×14.

Figs 6–9, 11–14. *Turrilepas wrightiana* (de Koninck). 6–9, 11, BM(NH) I16282, the anterior end of an assemblage, Wenlock Limestone, Dudley, Middle Silurian; 6, detail of anteriormost sclerites, ×4·5; 7, dorsolateral view of medial aspects of inner sclerites, ×2·5. 8, dorsal view, ×2; 9, right lateral view, ×2·5. 11, view of lateral aspects of inner left sclerites, ×4·5. 12–14, BM(NH) 47871, a disturbed anterior end of an assemblage. Wenlock Limestone, Dudley, Middle Silurian; 12, the anteriormost sclerites, exposed by Withers, see text for explanation, ×8; 13, dorsal view, ×2·5; 14, left lateral view, ×2·5.



ADRAIN *et al.*, *Turrilepas modzalevskae*, *T. wrightiana*

series, and there seems to be a fairly constant relationship between the size of the sclerite and spacing of the rugae. All of this indicates that the scleritome very likely had a fixed number of segments, and that growth was incremental, with rugae deposited one at a time, at the same time for all sclerites in the assemblage. The pattern observed is incompatible with serial addition of segments. This information, if it can be corroborated through further study, has important implications for reconstruction of machaeridian scleritomes when only disarticulated sclerites are available, the general case in the palaeontological record. If this relationship holds true, it can effectively be assumed that conspecific sclerites with a roughly equivalent number of rugae can be accommodated together in the same scleritome reconstruction.

Turrilepas modzalevskae sp. nov.

Plate 2, figs 1–5, 10

Etymology. For Dr T. L. Modzalevskaya.

Holotype. BM(NH) In63310, a unique specimen from the Konovka Formation (lower Ludlow), Podolia (for detailed locality see above), comprising parts of four segments from the mid-body of an articulated sclerite assemblage.

Diagnosis. A species of *Turrilepas* with extremely small, closely set marginal spines, five to seven between rugae of inner sclerites; I_1 crisply defined, about 100 degrees; at least twenty-eight rugae on mature sclerite; accreting margin of outer sclerites about two-thirds to three-quarters length of longitudinal angle.

Remarks. *Turrilepas modzalevskae* may be distinguished from *T. wrightiana* by a greater number of smaller, more closely spaced marginal spines, rugae which tend to run straighter between inflections, making the inflections slightly sharper, and especially by outer sclerites with accreting margins that are much shorter relative to the length of the longitudinal angle, giving the sclerites a less erect, more anteroposteriorly elongate appearance.

The specimen consists of an articulated portion of a sclerite assemblage, probably from some point along the undifferentiated midbody area. Very little displacement has occurred among those sclerites present, and the spatial relationships between sclerites appear to reflect those prevalent during the life of the animal. The specimen comprises two nearly complete and three partially complete inner right sclerites (the posteriormost having slipped medially to lie behind the sclerites of the inner left series), three nearly complete outer right sclerites, one nearly complete and two partially complete inner left sclerites, and one partially complete outer left sclerite.

Genus DELTACOLEUS Withers, 1926

Type species. *Deltacoleus crassus* Withers, 1926, from the Caradoc of the Balclatchie Group, Girvan, Ayrshire.

Other species. None.

Remarks. Withers (1926) established *Deltacoleus* as a monotypic genus, based upon only five disarticulated sclerites. Two were inner sclerites from the Upper Ordovician (Carodoc) of Balclatchie, one of which he selected as the holotype. Three were outer sclerites from the Middle Ordovician (Llandeilo) of Aldons. The holotype (Pl. 1, figs 1–3) is reasonably well preserved, but is missing most of its left non-accreting margin. It is an inner right sclerite, and has a distinctive morphology as follows: medial area about three-quarters the size of lateral area, compared with about one-half in *Turrilepas*; longitudinal axis gently curving, compared with essentially straight in *Turrilepas*; I_1R quite angular, not as broadly curving as in *Turrilepas*; I_2R very shallow, occurring on medial area, while deep and placed at or lateral to the longitudinal angle in *Turrilepas*; I_3R occurring on longitudinal angle; I_4R and I_5R spaced respectively about one-third and two-thirds of

the way between longitudinal angle and medial non-accreting margin, both shallow; at least thirty-six rugae; apical portion of sclerite slightly beaked.

The second inner sclerite, from the inner left series, is represented by internal and external moulds (the external mould figured in Plate 1, figure 6, the internal figured by Withers 1926, plate 6). While it shares a curving longitudinal axis with the first sclerite, it is otherwise much larger and of quite different appearance, with I_1L placed very near to the longitudinal angle, and I_2L–I_5L all occurring on the lateral aspect of the sclerite, as in *Turrilepas*. This sclerite is almost certainly not conspecific, and probably not even congeneric, with the holotype.

The outer sclerites are from much older rocks. The example figured by Withers (1926, pl. 8, fig. 8) is an internal mould with a fragment of sclerite material preserved of a left outer plumulitid sclerite. Withers (1926, p. 44) declined to refer it to the plumulitids because the specimen lacked a longitudinal fold, a feature he considered diagnostic. As is evident from the rephotographed specimen (Pl. 1, fig. 9), a weak dorsal inflection is present, consisting of two 'longitudinal folds', one at the midpoint between the non-accreting margins and one placed near the medial non-accreting margin, with the thickness of the sclerite inflected slightly dorsally between them. Comparison of the sclerite with the as yet undescribed silicified sclerite of Text-figure 1E confirms that it belongs within the Plumulitidae.

Hence, *Deltacoleus* appears to have been erected as something of an odds-and-ends taxon. Clearly, the concept of the genus must be based solely upon Withers's holotype. This is an unsatisfactory basis for comparison and more material would be required from the type area to properly delineate the taxon. The sclerites figured by Schallreuter (1985, pl. 1, figs 2–5) as *Deltacoleus erraticus* and *Deltacoleus? crenulatus* bear little resemblance to the holotype, and should be excluded from the genus. Schallreuter's (1985, pl. 1, fig. 1) *D.* cf. *crassus* is very similar to the holotype. This single sclerite certainly belongs to *Deltacoleus*. Whether or not it is conspecific with *D. crassus* can only be determined through further collecting of both the Scottish and German material. Dzik (1986, fig. 7) has figured three specimens from the Llanvirn and Arenig of Poland as *Deltacoleus* cf. *crassus*. The Llanvirn specimens (Dzik 1986, fig. 7A, B) seem conspecific (they are from the same erratic boulder), and may belong to *Deltacoleus*, although likely not to *D. crassus*. The affinities of the Arenig fragment (Dzik 1986, fig. 7C, D) are indeterminate.

In sum, before this genus can be of any use in comparative phylogenetic studies, thorough redescription of all its possible members will be required.

Genus CLARKEOLEPIS Elias, 1958

Type species. Designated herein as *Clarkeolepis clarkei* Elias, 1958, from the Mississippian Redoak Hollow Formation of Oklahoma.

Remarks. Elias (1958) described three machaeridian species, *Turrilepas whithersi* (discussed above), *Clarkeolepis clarkei*, and *C. elegans*. As he did not name a type species for the genus, *C. clarkei* is selected herein by virtual tautonomy and pagination. *C. clarkei* is known from two figured sclerites, and *C. elegans* from one. All three are likely conspecific, and hence *C. elegans* should likely be considered a subjective junior synonym of *C. clarkei*.

The sclerites assigned to *Clarkeolepis* are certainly machaeridians, but are characterized by a very low number of rugae (about ten), and an odd raised ornament apparently transecting the spaces between the rugae. More material and more thorough treatment is needed before any taxonomic conclusions, save to assert that the sclerites seem to belong in the Turrilepadidae, can be reached.

Genus SPINACOLEUS Schallreuter, 1985

Nomenclatural note. Schallreuter (1985) used the genus name *Spinacoleus* in his text, but *Rugacoleus* in the explanation of his figures. Article 24(*b*) of the ICZN requires that the first reviser cites the alternative names

together and chooses one as the correct name. Dzik's (1986) listing of *Spinacoleus* did not fulfil this requirement and is therefore not binding. In the interests of nomenclatural stability, however, *Spinacoleus* is selected here as the valid name.

Type and only species. Spinacoleus breugmanni Schallreuter, 1985, from Öjlemyrflint erratic boulder No. G16.

Remarks. The holotype and paratype material (Schallreuter 1985, pl. 2, figs 1–3) is poorly preserved. As mentioned above, the sclerite margins are missing from this material, giving the false impression that the rugae are extended into marginal spines. A more accurate impression is given by the better preserved sclerites questionably assigned to the species by Schallreuter (1985, pl. 2, figs 4, 6, 7), in which the rugae clearly terminate short of the sclerite margin, and the marginal spines are distinct and not spaced in any set relation to the rugae.

Schallreuter's (1985) material is without question properly associated and belongs to a distinctive turrilepadid form. Although it remains inadequately known, *Spinacoleus breugmanni* is sufficiently well described to allow comparison with other machaeridians. Hence, further work on machaeridian taxonomy may lead to a better understanding of this genus.

Genus MOJCZALEPAS Dzik, 1986

Type and only species. Mojczalepas multilamellosa Dzik, 1986, from Llanvirn strata (*E. reclinatus* Zone), Mójcza Limestone, Holy Cross Mountains, Poland.

Remarks. Dzik (1986, fig. 5) figured only two fragmentary and poorly preserved inner sclerites when he erected this taxon. Unfortunately, these sclerites give no satisfactory idea of the structure, shape, or pattern of rugae of the originals. As such, there does not seem to exist an objective basis for reference of further material to this taxon or for comparison with other turrilepadid forms. Satisfactory incorporation of this taxon into a general scheme of machaeridian classification must await adequate redescription and illustration.

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